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GENERAL BIOLOGY

Lemmings of Bolshevik Island (the Severnaya Zemlya Archipelago) is a Relict of the Last Glacial Epoch

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The intraspecific variation of various taxonomically important characters in lemmings from the genus *Dicrostonyx* in the Palearctic region has been studied repeatedly [1–3]. It is generally accepted to distinguish two lemming species in this region, *Dicrostonyx torquatus* Pallas, 1779 and *D. vinogradovi* Ognev, 1948. The geographic range of the latter species is restricted to Wrangel Island. Within *D. torquatus*, two continental subspecies are distinguished (*D. t. torquatus* Pallas 1779 and *D. t. chionopaeus* Alien, 1914, whose ranges are separated from each other by the Yenisei River) and one insular subspecies, *D. t. ungulatus* Baer, 1841 inhabiting the Novaya Zemlya. The taxonomy of lemmings from the Severnaya Zemlya remains unclear for the lack of material. V.N. Kalyakin (Geographical Faculty, Moscow State University) kindly provided us with representative material from the pellets of polar owls collected at the southern extremity of Bolshevik Island in 1983. This material contained 17 fragments of skulls with teeth (complete and incomplete rows), 46 lower jaws (also with complete and incomplete tooth rows), and individual teeth M_1 26; M_2 12; M^1 16; M^2 11; M^3 11.

In the modern and fossil lemmings of the genus *Dicrostonyx*, the structure of the molar masticatory surface varies. The analysis of paleontological material showed that different variants predominated in different periods of the genus history [4]. On the basis of this evidence, several successive species forms have been described. *D. simlicior* is assumed to be typical of middle Pleistocene, whereas *D. henseli*, of late Pleistocene. Variants with pronounced additional triangles on molars are considered apomorphic. The rate of the evolutionary transformation of the first and second upper molars is known to be much higher than that of other teeth. A tooth was assigned to a definite morph by measuring the corresponding angle using a technique described previously [2], with some later modifications; the criteria were the same for the first and second teeth. A larger angle corresponded to a better developed additional triangle. The scale factor of the sizing tool was 5° and the entire range of measurements was 0°–120°. The designation *sim* corresponds to the morph, typical of *D. simplicior*, that lack any newly formed triangles. The morphs typical of *D. heseli* (*hen*) corresponded to angles from 5° to 50°. Large angles corre-

Table 1. The frequencies of tooth morphotypes *torquatus*, *henseli*, *simplicior* (%) in the samples of Dicrostonyx from Bolshevik Island of the Severnaya Zemlya archipelago

Tooth	Side	*N*	*simplicior*	*henseli*	*torquatus*
M^1		39	0	90	10
M^2		32	0	69	31
M^3	Ling.	23	30	70	0
	Lab.		39	61	0
M_1	Ling.	52	23	77	0
	Lab.		0	89	11
M_2		40	–	0	100
M_3		37	–	100	0

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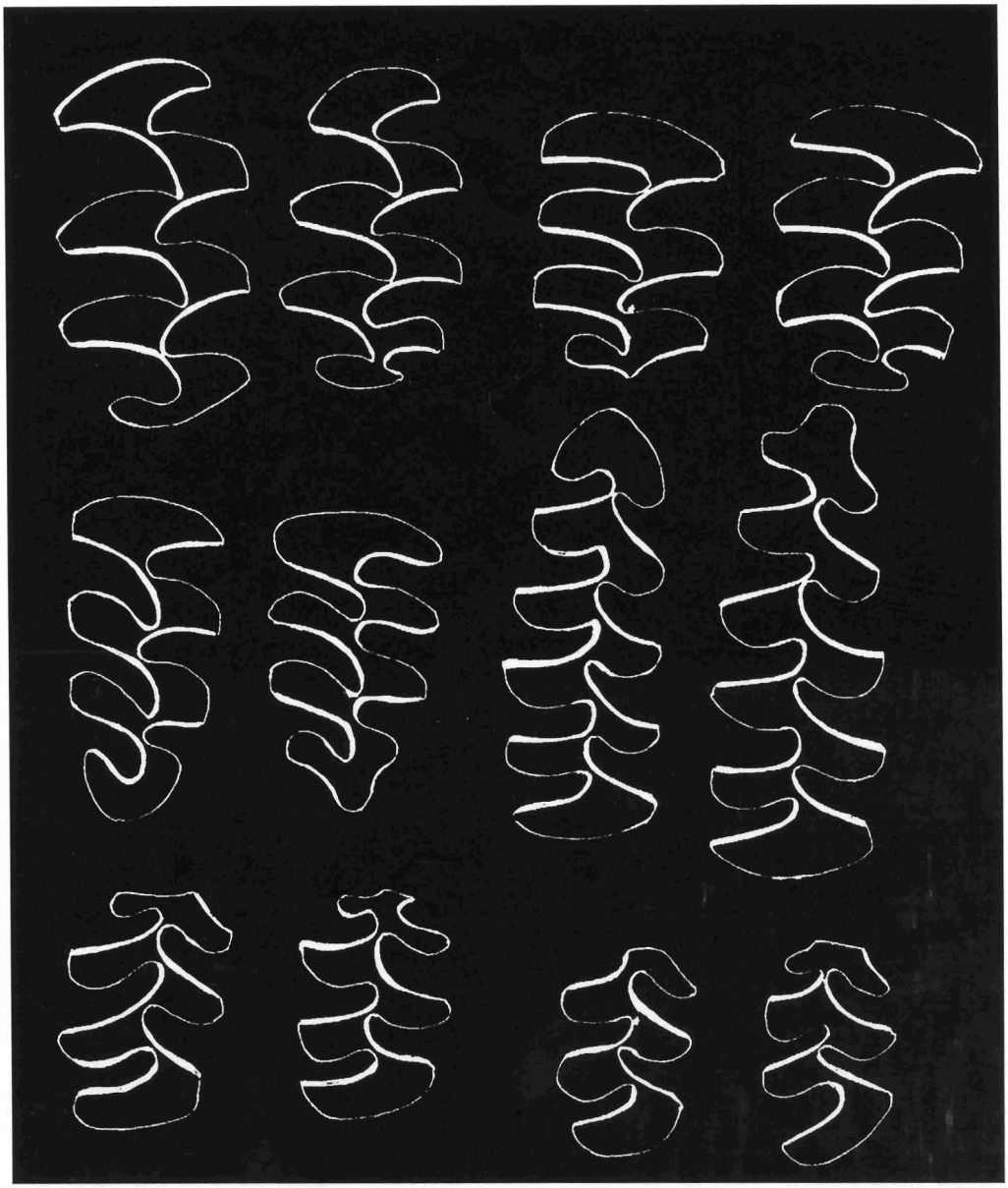

Fig. 1. Variation of the masticatory molar surface in *Dicrostonyx* from Bolshevik Island. Extreme variants are shown: on the left, the most primitive variants; on the right, the most advanced variants of the structure of each tooth. The arrows indicate variable tooth regions. (*1*) M^1; (*2*) M^2; (*3*) M^3; (*4*) M_1; (*5*) M_2; (*6*) M_3.

sponded to the interval of morphs characteristic of *D. torquatus* (*tor*). In this study, the variation range was divided into five morphs for the first tooth and five morphs for the second one (0°, 5°–25°, 30°–50°, 55°–75°, and 80° or higher corresponded to morphs *sim, hen1, hen2, tor1*, and *tor2*, respectively).

The morphs of the other teeth, namely, the upper third tooth and all lower teeth, were differentiated as described previously [2]. In lemmings from Bolshevik Island, the *henseli* tooth morphotypes predominated except for the second lower tooth (Table 1). All M_2 teeth from our material had the *torquatus* morphotype. The *simplicior* morphotype was the second most frequent for the third upper tooth and the first lower one on the lingual side. This tooth structure is not characteristic of the modern Eurasian *Dicrostonyx* (Table 2). The most important feature of modern lemmings from Bolshevik Island is that the *henseli* morphotype predomi-

Table 2. The frequencies of morphs for the first and second upper molars in the samples of Dicrostonyx from Bolshevik Island of the Severnaya Zemlya archipelago and from other regions of northern Asia

Morph	Angle (degrees)	Yamal		Severnaya Zemlya		Taimyr		Chukotka	
		M^1	M^2	M^1	M^2	M^1	M^2	M^1	M^2
		$N = 106$	$N = 239$	$N = 39$	$N = 32$	$N = 68$	$N = 68$	$N = 63$	$N = 74$
Sim	0	1	1	0	0	0	0	0	0
Hen1	5–25	14	11	59	44	3	1	1	1
Hen2	30–50	14	11	31	25	15	6	9	7
Tor1	55–75	45	48	10	25	46	27	28	16
Tor2	80–115	26	39	0	6	37	66	62	76

nates in their first and second upper teeth, which is characteristic of late Pleistocene lemmings (Fig. 1).

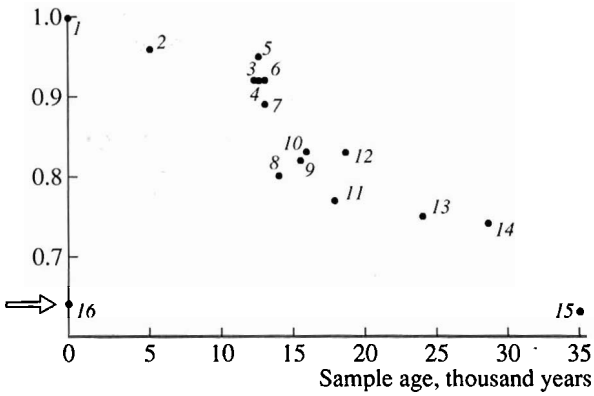

Fig. 2. The relationship between the age of fossil lemmings of the genus *Dicrostonyx* and the *r* similarity index between these forms and modern lemmings from the southern Yamal (the mouth of the Payuta River); the samples of modern lemmings from Bolshevik Island are included (no. 16); calculations have been made from the frequencies of the M^1 and M^2 upper molars. Points *1–7* correspond to fossil locations of *D. torquatus*; *8–15*, to those of *D. guilielmi*. Below, *n* (the number of teeth measured), years of radiocarbon age, laboratory index, and the sample number are indicated for each sample. (*1*) modern *D. torquatus* from predator pellets, southern Yamal (the Payuta River mouth, $n = 392$); (*2*) the Arakaevo-8 cave, digging 1, $n = 39$, 5 568 ± 300 years (IEMEZh-202) (*3*) the Rasik grotto, horizon 21, $n = 340$, 12680 ± 180 years (GIN-10569); (*4*) Kakva 4, $n = 41$, 12800 ± 300 (GIN-9444); (*5*) Dyrovatyi Kamen' on the Chusovaya River, $n = 225$, 12 820 ± 60 (CAMS-35894); (*6*) Rasik, horizon 24, $n = 418$, 13 250 ± 120 (GIN-10568); (*7*) Rasik, horizon 27, $n = 378$, 13 330 ± 120 (GIN-10567); (*8*) Bobylek, layer 2, $n = 54$, 14 200 ± 400 (Institute of Plant and Animal Ecology-164); (*9*) Arakaevo-8, digging 2, horizon 12, $n = 65$, 15 739 ± 590 (IERiZh-230); (*10*) the Medvezh'ya cave, a layer of brown loam, $n = 156$, 16 130 ± 150 (LE-3060); (*11*) the Medvezh'ya cave, a layer of brown loam, $n = 59$, 17 980 ± 200 (LE-2876); (*12*) Cheremykhovo-1, site 4, $n = 185$, 18 784 ± 379 (IEMEZh-1259); (*13*) 430 km from the Ob' River mouth, $n = 81$, 24 000 ± 150 (IERiZh-63); (*14*) Cheremukhovo-1, site 1, horizon 54, $n = 53$, 28 520 ± 850 (AA-36469). (*15*) Betovo, $n = 225$, 36100 ± 500. (*16*) The arrow indicates the index of similarity to lemmings from Bolshevik Island.

The index of population similarity in polymorphic parameters (*r*) [5] was evaluated to compare the samples qualitatively. In the cases of a complete similarity or dissimilarity *r* assumes values 1 and 0, respectively. In a series of tooth samples from fossilized remains of *Dicrostonyx*, whose age was determined by the radiocarbon method, the parameters of similarity were calculated and compared with those of the reference modern sample, and the position of lemmings from Bolshevik Island in this series was determined. The reference sample included skulls from pellets of predatory birds near the Payuta River mouth in the southern Yamal Peninsula near the Polar Urals. Figure 2 shows the results of this comparison for fossils of different ages.

Our calculations showed that the morphs of the first and second upper teeth of modern lemmings from the Bolshevik Island are most similar to those of fossil lemmings from the Betovo site (with the fossil age about 36 000 years), which suggests that the former lemmings are a relict of the last glacial epoch.

Lemmings with the tooth system similar to that of the fossil ancestors were previously found among the modern lemmings of North America. A peculiar species *D. hudsonius* with a molar form similar to that of the mid-Pleistocene *D. simlicior* inhabits the shores of Hudson Bay. Samples of *D. groenlandicus* from some Canadian Arctic islands with the structure of the tooth system characteristic of the last glacial period have been recently described [6]. Thus, the lemmings from Bolshevik Island may be positioned in the series of relicts between *D. hudsonius* (an analog of mid-Pleistocene forms) and the archaic *D. groenlandicus* (an analog of lemmings of the last glacial period).

Why the relict late-Pleistocene form of *Dicrostonyx* is preserved on Bolshevik Island? The explanation for this phenomenon might lie in the history of the archipelago during the past 550 000 years. D.Yu. Bol'shakov and V.M. Makeev have hypothesized that glaciers have no significant effect on the relief and deposit formation in the Severnaya Zemlya archipelago [7]. Even the

maximum late-Pleistocene (Sartan) and young Holocene glaciations did not covered the islands completely. Covering glaciations are most likely to have occurred earlier, 90000 to 70000 years ago. The specific natural and climatic development of the Severnaya Zemlya during late Pleistocene explains the fact that the mammoth fauna complex, instead of migrating to the south, migrated slightly northwards compared to the Kargin interglacial period [7], and the isolation from the continent lasted for at least 12 000 years.

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